

EVOLUTIONARY ORIGIN OF BEES
(HYMENOPTERA: APOIDEA)

U. N. Lanham

Abstract.—Bees are generally supposed to be descendants of sphecids wasps, largely on the basis of similarities in thoracic structure. If it be assumed that these similarities are convergent, resulting from independent evolution for high-precision flight, then an argument can be made for a close relationship between bees, ants, and scolioid wasps.

In 1951 I wrote that "the pollen and nectar-feeding bees arose from the primarily predaceous wasps . . .," even then a well-worn phrase, and went on to say that ". . . but acceptable theories as to the transition between the two modes of life have not been worked out." This last also was true then and is now, in spite of the publication of a book on the evolution of the Hymenoptera (Malyshev, 1968). Nor does the present paper remedy the situation, in the sense that "at last the mystery is solved." Nevertheless aculeate phylogeny, although an inherently frustrating subject, in the manner of all phylogenetic studies, is worthwhile insofar as it organizes observation of the immense complexity of morphology and behavior to be found in the aculeate Hymenoptera.

It is the modern consensus that the group of wasps that gave rise to the bees is the sphecids. Two recent works supporting this theory are those of Bohart and Menke (1976:31) and Brothers (1975). Among the sphecids, Malyshev (279ff) selects the pemphredonines as the group offering a transition from sphecid to bee. Some of these are small wasps nesting in twig cavities that they fill with small, soft-bodied insects such as aphids. Individual cells along the length of the twig cavity are lined with a tough transparent membrane produced by mandibular glands of the female. The most wasp-like of the bees, according to Malyshev, are the hylaeines, some of which also nest in twig cavities with individual cells lined by thin transparent membranes. Aphid-feeding pemphredonines, Malyshev reasons, could have shifted from aphids, themselves a mixture of protein and honeydew, to a pollen-nectar food store for the young. This would mark the genesis of bees.

Hylaeine bees and pemphredonine wasps resemble each other both superficially and in those characteristics, mainly involving the thorax, which in Brothers' opinion tie all of the bees closely to the sphecids. A discussion of these common characters will be deferred for the moment to concentrate on the differences. If a *Hylaeus* is examined carefully at high magnification, it will be found that at least a few of the hairs are compound (branched or

feathery). Such hairs are especially abundant in the short filter fringe on the prothoracic lobe, which covers a large spiracle. Hylaeine bees are somewhat atypical in being relatively hairless; most bees are abundantly long-hairy, with many branched hairs. In fact, the presence of branched hairs is absolutely diagnostic in comparing bees with sphecids: none of the sphecids have such hairs; all bees do have them.

It is unreasonable, in my opinion, to think that the few compound hairs of the hylaeines represent a basis for the selective evolution of compound hairs in the bees. Rather, they represent the situation found in the many species of parasitic bees which do not have to transport pollen in external baskets or brushes; these are also nearly hairless, and also have a few compound hairs. Hylaeines transport pollen to the brood cells in the crop, gathering the pollen with their front legs into the mouth. It seems more reasonable to think that they display a specialized reduction of hairs such as occurs in the parasitic bees, made possible by the crop-transporting mode. Better representatives than the hylaeines of primitive bees are perhaps the euryglossines, limited to Australia, which are not superficially wasp-like. Although these, like hylaeines carry pollen in the crop (presumably the primitive mode) rather than externally, they are abundantly long-hairy, with many compound hairs. The hylaeines could then be regarded as specialized descendants of the euryglossines.

It is difficult to imagine that the presence of a few compound hairs in the manner of the hylaeines would provide the broad and stable base necessary for the evolution of compound hairs which, judging from their absolute absence in the many thousand species of sphecid, vespids, pompilids, tiphiids, and scoliid wasps, are not evolved except in highly unusual circumstances (Lanham 1979). If we take the compound hairs as representing a fundamental rather than trivial character of the bees, then we are led to consider the possibility that the pemphredonine-hylaeine transition is not the best hypothesis for the evolutionary origin of bees.

Another difference that leads to the same conclusion is one which for some reason escaped general notice until rather recently (Lanham 1960 and Bohart and Menke 1976:27). This is the presence on the hind leg of the sphecid of a strigil composed of a hind tibial spur (sometimes modified) facing a brush-lined concavity at the proximal end of the basitarsis. When the wasp disposes of particulate debris, it pulls the opposite hind leg, which is stocked with the particles by a variety of grooming movements, through the strigil in the manner that the antenna moves through the strigil of the front leg. In all bees the hind strigil is absent, and debris is disposed of by shuffling together the two brushes on the inner surfaces of the widened hind basitarsi. It has been suggested that the evolution of the basitibial brush in the bees obliterated the ancestral sphecid strigil, but it seems to me that the brush is a character which has been inherited directly from primitive astrig-

then the similarity in thoracic structure must be regarded as the result of convergent evolution. Brothers, who has made a detailed study of the aculeate thorax in his phylogenetic studies, finds three characters of the thorax which in his numerical procedure tip the balance heavily in favor of a close bee-sphacid relationship.

1. The antero-lateral corner of the mesoscutum is enlarged so that it extends far anterior to the tegula. This is Brothers' character state 21.2, which "arose uniquely on internode 4-5 and thus is a very good indicator of the holophyly of the sphacid and apid groups." The position adopted here is that it arose on two occasions, once within the strigilate wasps, once within the astrigilate wasps.
2. The ventral angles of the propodeum are slender and so elongate that they almost or quite encircle the thorax, meeting (or nearly so) at the ventral midline. This is character state 23.2, which "is uniquely present in the sphacid and apid groups and apparently arose on internode 4-5, thus forming a strong indicator of the holophyly of this grouping." The position taken is that this structure is the inevitable consequence of the enlargement of the antero-lateral corners of the mesoscutum. There is no other way in which a broad support to brace the prothorax (which carries the industrially important front legs) against the mesothorax can be managed, when the slanting abutment against the anteriorly narrowed mesoscutum of other aculeates is abolished. Thus character state 23.2 is a mechanical correlate of 21.2 and cannot be weighted as a separate evolutionary event.
3. The origin of the postphragmal muscle shifts posteriorly to a position on the dorsal surface of the apparent propodeum. Brothers interprets the origin of this muscle as always being the metapostnotum, so that the large "triangle" of the propodeum is the metapostnotum. This is character state 35.3, which he says is "unique in the Aculeata and apparently in the Hymenoptera as a whole. This remarkable modification of the metapostnotum which is present in the sphacid and apid groups provides extremely strong evidence of the holophyletic association of these groups, having arisen on internode 4-5." The small postphragmal muscle inserts on the posterior surface of the 2nd phragma, a curved sclerotized band whose anterior face provides the area for the origin of the longitudinal indirect flight muscles. In character state 35.3 the phragma becomes vertical instead of slanting far back of and below the insertion of the postphragmal muscle (Brothers 1976, figs. 1-12). When the phragma became vertical, the bundles of the longitudinal muscles become more nearly equal in length, and the functional center of the phragma has retreated, making necessary a posterior shift in the origin of the postphragmal muscle. I am unable to explain the functional significance of

this, except to say that it would seem reasonable that equal-length longitudinal fibers would deliver more smoothly the power that arches the mesoscutum and depresses the wings. At any rate, the net result of all three character states is the consolidation of the indirect flight muscles (which furnish nearly all of the energy of flight) into a compact subspherical or elliptical mass. It may be that character state 35.3 is also part of the only solution to the problem of enhancing flight ability (a matter to be discussed in the next section) and thus, like state 23.2, not to be weighted as independent of the other two character states.

Enlargement of the antero-lateral corners of the mesoscutum is here taken to be the basic morphological character from which other major thoracic characters follow. Its primary function is that of increasing the area of insertion, hence the size of the vertical (elevator) indirect flight muscles. Judging from the figures of the thoracic musculature of *Apis* in Snodgrass (1942) the longitudinal and vertical muscles are of equivalent size. This would mean that the upstroke would deliver approximately the same power as the downstroke. This aspect of the functional morphology of the aculeate thorax is a complex subject that has not been investigated. However, nearly every field entomologist has seen the extreme example: the large anthophorine bees or the bembecine wasps, which hover perfectly still, then accelerate swiftly to a speed where they become invisible (an object this size becomes invisible at about 35 miles per hour) and with such accuracy that they easily avoid the net. No other aculeates approach the powerful and high-precision flight of such bees and sphecids. Intuitively it would seem that continuous delivery of power at a uniform level would give an aerodynamic fine-tuning not attainable in the presumably more ragged flight of a wasp with a considerable difference in delivery of power in upstroke and downstroke. The effect on flight musculature of the anteriorly narrowed mesoscutum (characteristic of all aculeates above the bethyloid level except sphecids and bees) can be seen in the figures by Duncan (1939) of the thoracic musculature of the vespid wasp *Vespula pennsylvanica* (Sauss.). Here the longitudinal indirect flight muscles are, says Duncan, enormous, being much the largest muscles of the body. The size of the vertical muscles, which insert laterally on the mesoscutum, is limited by the shortened area for insertion as compared with the longitudinals. Some tiphiid and pompilid wasps seem to have the anterior portion of the mesoscutum squared off rather than narrowed, but this is illusory. If the long, overlapping pronotal collar is pried off, underneath can be seen the sclerotized, narrowed end of the mesoscutum.

In brief, it is proposed that a major adaptive characteristic was arrived at independently in the bees and sphecids. This adaption is the high-precision flight made possible by the enlargement of the elevator flight muscles. In

the bees, this is useful in flower visiting and return and entry to a nest. In the sphecids wasps it is useful in visiting flowers for fuel, searching for and catching prey, and returning to and entering a nest. In both it is, especially in the spacious, competitive desert environment, helpful in eluding birds or such swift insect predators as asilid flies or, indeed, some of the sphecids wasps themselves.

With the bees now in theory detached from the sphecids, a possible home for them is provided in the accompanying phylogenetic tree. Letters indicate major strategies or adaptive advances that separate the tree into a number of sectors, each of which contains one or more higher taxa.

Bethyloids (sector 1) are for the most part small to minute parasitic wasps. These probably could not be directly ancestral to any of the aculeate groups with large-sized individuals, since wing venation is much reduced in the forewings and absent in the hindwings. The genus *Scleroderma* of the bethylids has long figured in speculations on the origin of ants (see Malyshev p. 217ff). A female lays many eggs on a large host larva and stays with it, providing rudimentary care for the young. Eventually a few generations of wasps are present on a single larva, forming a pre-social aggregation including many wingless, ant-like females. The phylogenetic position of the bethyloids is not well understood, but they have a mixture of characters belonging to other superfamilies, so could possibly be specialized descendants from a primitive stock of aculeates.

Strategy A is a modification of the parasitic mode in which relatively large and powerful wasps dig through loose soil or rotting wood in a more predatory fashion after beetle larvae which they paralyze with the sting, and on which they lay a single egg. Primitively they leave the prey in place, but some dig a cell which shelters the larva and the subsequent wasp larva, or even move the host larva to another shelter. Sector 2 includes two major families, the scoliids and tiphiids, which are particularly abundant in the warmer parts of the world and with many species in the Southern Hemisphere. These families, and two or more smaller families, are sometimes put in a superfamily, the Scolioidea. They can be termed the non-nesting astrigilate wasps, although as already pointed out, the behavior of some of the species grades into the better defined nesting behavior of the more advanced wasps.

Strategy B is an adaptive shift in which some of the astrigilate wasps use arboreal nesting sites where they store prey in cavities in wood. These clean and dry sites in the tropical forest might have proved a major new nesting environment which made possible a train of events leading to the ants and bees. These nesting cavities, which would be enlarged, using the mandibles, were from the beginning, and remained so during the early stages of bee evolution, communal nest chambers. This communal mode leads easily into progressive feeding, then through pre-social communities to true societies. One of the consequences of moderately large societies, it seems to me, must

have been the opportunity to widen the food base. Primitive hunting wasps, for example, might be transformed from fairly specialized hunters into general hunters and scavengers, bringing all kinds of edibles into the nest. In some instances, the at first tentative use of a new food source might open up an area for specialization. While most modern ants, for example, are generalists, a few are specialists on such prey as other ant species or terrestrial isopods. Social aculeates living in communal nests produce a significant evolutionary event—larvae with long hairs (Lanham 1979). Long-haired larvae, otherwise unknown in the aculeates, occur in about 90% of the genera of ants and in many of the genera of allodapine bees. Furthermore, at least one species of allodapines and about half the genera of ants have compound larval hairs. The modified hairs of ant larvae have a greater variety of form than any other feature of ant morphology. Some 30 types have been described and appear to be adaptations for various characteristics of life in communal cells (Wheeler and Wheeler 1976). Communal nests (with only a handful of apparently irrelevant exceptions) are known among the aculeates only in the ants (essentially all) and in some bees (some allodapines and *Bombus*). Thus, the bees have been placed in a phylogenetic milieu that could explain the two features separating them from the sphecids: absence of the hind strigil and presence of compound hairs.

Nowhere have there been found scolioid wasps that suggest the kind of transition made in strategy B. There is only one extensive, unexplored group remaining among the larger scolioid wasps. This is the subfamily Thynninae, with about 500 species in Australia and some hundreds in South America. All the known species have winged males and wingless females. Males are larger than the females and carry them about during mating. For most species, the females are observed only when found on the conspicuous, flower-visiting males. Some spend most of their time burrowing about in the ground in search of beetle larvae. Probably the biology of fewer than 5% of the species is known in Australia (Burrell 1935). The females of these sting the host larva, oviposit, and leave it in place. In only one species, which is taxonomically isolated from the rest of the thynnines (*Diamma bicolor* Westwood) is the female known to drag its prey to its own burrow. In species other than *Diamma* the males, unlike nearly all other aculeates, play a role in the economy of the wasp other than fertilizing eggs. Some carry the females, attached to the tip of the male abdomen, to feeding sites, either flowers or honeydew-secreting scale insects, where they position themselves so that the female can drink. Others carry nectar or honeydew to the female, carrying a droplet in a basket of hairs on the underside of the head (Given 1954), or feeding by regurgitation. Perhaps somewhere in this ancient and abundant group there may be found small societies of females (even attended by solicitous males) which would bear witness to the former existence of sector 3. A few species live in wood.

This is the place to point out that the delineation of a clean, arboreal

communal nesting site as the site for the evolution of the ancestral stock of bees may have fashioned a two-edged sword, which may provide evidence that it was indeed the sphecids wasps that gave rise to the bees. It has been rather recently discovered (see Matthews 1968 and Bohart & Menke 1976:172) that a genus (*Microstigmus*) of small neotropical pemphredonine wasps live in diminutive (18×12 mm) bag-like nests suspended from the underside of the leaves of forest trees. The species *M. comes* Krombein, measuring about 3 mm in length, constructs the nest from fibers scraped from the undersurface of the leaf. It would seem that this cavity would offer the ideal opportunity for the establishment of a communal nest, yet this species remains determinedly sphecid, constructing in the loose fibers filling the lower half of the bag up to 15 separate cells, with one naked larva reared in each. Nevertheless, one can imagine that in the yet unstudied species of the genus there may be found an evolutionary sequence in which cell making is abandoned and the larvae have become hairy, in the manner of other aculeates living communally. Only 17 species of *Microstigmus* are listed in the Bohart and Menke catalogue, but apparently more than a hundred more have since been discovered. These wasps represent a most interesting departure from the biologies of other sphecids, but it is probably a specialization too recent to have been involved in the evolution of the bees or ants or both.

Strategy C was the commitment to on-foot foraging by a wingless female worker caste. Reproductive males and females are generally winged, but flight ability is degenerate, serving to form mating swarms and to aid in dispersal. This social, on-foot foraging mode of existence laid the foundation for the evolution of the most successful group of aculeates, the ants, with a number of species exceeded only by the bees and in numbers exceeding all other aculeates. Although they are dominant in the arboreal fauna of the tropics below 2,500 meters of altitude, the key to their success has been the invasion of the nutrient rich ground-air interface, where they rule in all the sunwarmed land environments on the earth.

Sector 4 is the living family Formicidae, the ants. In the clean arboreal environment there was no selection of the hind strigil and the ants remained almost entirely astrigilate. A few of the ground-dwelling genera, such as *Neoponera*, have a fairly well developed hind strigil, but these occur in only few and scattered instances, and are taken to be independent origins of this structure. The other thousands of species of ground dwelling astrigilate ants are able to take care of hygiene by mutual grooming and the fact that the legs are so long that the hind legs can be pulled through the strigil of the front legs.

As has been said, probably about half the genera of ants have larvae with compound hairs. A few species also have compound hairs in the adult stage. Two are known in North America. *Triglyphothrix striatidens* (Emery), an

introduced species, has trifold hairs. The larva has hairs with "multifid tips" (Wheeler & Wheeler 1973). The native species *Acanthomyops plumipilosus* (Buren) has plumose hairs, the genus itself generally has denticulate hairs as larvae. The similarity between larval and adult hairs, particularly in the peculiar first example, tends to support my contention (1979) that the genetic expression of compound hairs can be shifted from the larval to the adult stage. However, the numerous examples of exotic ants with odd shaped hairs in the adult need to be checked against larval morphology to learn more of this phenomenon.

Strategy D is a rather minor development in which the females usually become wingless and solitary parasites of the nests of other Hymenoptera. Some extra-North American species are said to parasitize larvae of other insect orders.

Sector 5. The great majority of species are in the family Mutillidae. The families Eotillidae, Typhoctidae, and Anthoboscidae (females winged) are included in this sector because at least some of the species of each have compound hairs, thought to be sporadic, genetically based reminiscences of a cavity-nesting past.

Strategy E is the specialization for pollen feeding that marked the origin of bees. One other group of aculeates, the masarine vespids, also provides its young with a food store of pollen, but this was a relatively small scale venture, involving less than a thousand species. Bees total about 20,000 species, and have more than any other group cooperated in the evolution of the flowering plants. As said in the discussion of Sector 3, the social mode makes possible a widening of the nutritional base. Among the edibles brought in to these early societies there would certainly be pollen, which was available in the Cretaceous, when these early phases in hymenopteran evolution were taking place (Evans 1973). Instances in which pollen becomes an important food source would produce overwhelming selective advantage for the changes in control genes that would transfer expression of compound hairs to the adult stage. The pollen-gathering masarine wasps, mentioned above, did not have a communal-nesting ancestry, never had compound hairs in their evolutionary background and the modern species do not have compound hairs.

Sector 6 comprises the bees, usually put in a superfamily divided into several families. Thus use of the term "apids" here is merely a convenience, following the terminology used by Brothers, and does not represent a statement as to the rank given the taxon. It is supposed here that the bees were primitively social arboreal cavity nesters. Today only a minority of bees are social, either primarily or secondarily, being represented by several hundreds of species, most of them dwelling in arboreal nests constructed of wax and resins, but the allodapines resembling at least superficially the supposedly primitive mode in which there are small communal nests in twig

cavities. Among the wax-nesting bees are the usually nonarboreal *Bombus*, of which a few species nest communally during at least part of the seasonal cycle. None of these have long-hairy larvae. In the more primitive bee societies, reversion of social bees to the solitary mode, or even the reverse, is quite feasible (Wilson 1971:102). The vast majority of living bees are solitary, are especially well represented in arid regions, and usually nest in the ground in the manner of many sphecids species, providing each larva with its own earthen cell.

Strategy F represents the transition between the primitive astrigilate non-nesters to the strigilate ground nesters. Here the burrow and the cells are carefully constructed, with a brood cell of compacted earth. The nest is often multicellular, thus being visited often between foraging trips, and even when unicellular, with several burrows being dug, the cell is often provided with several prey insects or spiders. It is here postulated that the development of the hind strigil is of adaptive value in keeping clean in this mode of life, and in helping maintain hygiene in the brood cells.

Sector 7 includes the pompilids (spider wasps) and vespids wasps. Pompilids are either ground nesters (sometimes using a preformed cavity) or construct above-ground nests of mud cells. All are solitary. They are rather poor fliers, and have a tendency to collide with rather than gracefully alight upon flowers. They tend to do much of their hunting on foot. The primitive subfamilies of the vespids are solitary, constructing their cells in the ground, or in twigs building mud cells above ground. The advanced vespine wasps build arboreal nests of papery materials (sometimes the same sorts of nests are made in large underground cavities). These wasps are always social. Each larva has a separate paper cell.

Strategy G involves the evolution of high-precision flight, the morphological expression being the expansion of the antero-lateral corners of the mesoscutum. It may be that the failure of this character to develop in the vespids was due to the evolution of the yet unexplained peculiarity of the wings, which in all but a few primitive forms are kept folded lengthwise when not in use. This might have some advantage in the nest life, but might well be a liability in flight. Its advantage in the sphecids is probably a reflection of their generally more intense foraging and nesting activity: the frequent visits to flowers for nectar for fuel, alternating flight and on-foot pursuit of prey, sometimes the prey captured in flight, and the wasp hovering alertly, ready to dash away at any disturbance.

Sector 8 includes the sphecids wasps. The biology of the exceptional social forms was discussed earlier. The thousands of species of solitary forms, mostly ground nesting, prey on insects or, more rarely spiders. Unlike the bees and scoliids, there are few endemic or aberrant groups in Australia.

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University of Colorado Museum, Box 218, Boulder, Colorado 80309.

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